

Kindred spirits: “*Brachythemis leucosticta*”, Africa’s most familiar dragonfly, consists of two species (Odonata: Libellulidae)

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ABSTRACT

Brachythemis leucosticta was found to include two morphotypes, which we consider to represent separate species. Males are separable by the ventral structure of S8 and often differ in the colour of the venation and genital lobe. Females are as yet not reliably distinguishable. Examination of 1,154 males demonstrated that both species are widespread: the true *B. leucosticta* occupies most of tropical Africa and Madagascar, while *B. impartita* (comb. nov.; corrected spelling — neotype ♂: Ngaoundaba Ranch, Cameroon; in RMNH) ranges north and south of the Sahara, and extends into Eurasia. The two overlap from The Gambia to Ethiopia and south at least to Lake Victoria. The presence of wing bands was scored for all examined males and 970 females. Banded females are frequent in sub-Saharan populations of *B. impartita*, but virtually absent in *B. leucosticta* and northern *B. impartita*. *B. impartita* males become banded shortly after emergence, but *B. leucosticta* becomes so more gradually. Larval morphology and ecology require further study, but some ecological and seasonal segregation may occur in areas of overlap. Of two larval forms described from Uganda, the ‘mud form’ may pertain to *B. leucosticta*, and the ‘sand form’ to *B. impartita*.

INTRODUCTION

Brachythemis Brauer, 1868 is a genus of stocky libellulids with conspicuously orange or brown marked wings. The five species currently included inhabit the warm regions of Africa and Eurasia, although *Deielia phaon* (Selys, 1883) from E Asia probably belongs to it too (Ris 1911b; Dijkstra 2003; Pilgrim & von Dohlen 2008). *B. leucosticta* (Burmeister, 1839) is one of Africa’s most familiar dragonflies. Mature males are easily recognised by their dark bodies and banded wings (Fig. 1). *B. leucosticta* extends into southern Europe, the Near East, and Madagascar, and can be abundant around larger water bodies, especially those with exposed banks with

sparse vegetation. Adults perch on or close to the ground, flying low over it, and may follow large animals – including humans – to prey on disturbed insects. Trailing big game on bare-trodden riverbanks, it may be the ultimate ‘African’ odonate. Indeed its abundance, behaviour, and striking appearance make it the most noted species among newcomers to the continent and the most ignored by those more ‘experienced’.

Philip Corbet (1999: 366) devoted two pages of his handbook and a paper with Peter Miller (Corbet & Miller 1991) to the ‘accompanying behaviour’ of *B. leucosticta*. Miller (1988) previously investigated its reproduction, while Corbet (1957, 1959) described the larva and found it the dominant adult odonate eaten by Ugandan Nile Crocodiles. The latter publications are from Corbet’s time on Lake Victoria in Uganda (1954-1962). Here, eager for specimens, he awarded one shilling for every dragonfly caught. However, ‘only’ lots of *B. leucosticta* were delivered and he quickly ended the scheme. Nonetheless, it now appears that what seemed endless series of the lake’s most ubiquitous and identifiable dragonfly, probably consisted of two superficially identical taxa (see Parr 2009).

Examining two syntopic Senegalese males, identified as *B. leucosticta* by the first author from photographs, the second author noted differences in the ventral structure of S8 and cerci. After ruling out lookalike *Parazyxomma flavicans* (Martin, 1908) (see Dijkstra 2003), a preliminary investigation showed that two types of males were distinguishable and widespread, occurring together locally. This paper details their characters, taxonomy, and distribution. It is dedicated to two kindred spirits, now both sadly departed, with a special relationship with Odonata, Africa, and *B. leucosticta*, Philip Corbet (1929-2008) and Peter Miller (1931-1996). Corbet & Miller (1991) were “indebted to the large African mammals which, by persistently moving slowly through grassland, served as targets for accompanying *B. leucosticta*.” As giants of odonatology they too progressed persistently, moving our science forward and inspiring those who flocked around them. Indeed, over thirty odonatologists contributed to this paper.



Figure 1: *Brachythemis impartita*, a species that was confused with *B. leucosticta* for 170 years. This male was photographed in Burkina Faso, where both species may occur together. Photo by Olivier Esnault.

MATERIAL AND METHODS

Distinguishing characters were determined from a series from Tanzania including both assumed taxa (61 males, 37 females, Mwanza, 1983-1986, leg. P.C. Goudswaard; in RMNH) and tested with material from elsewhere. With diagnoses established, numerous collections and colleagues (see Acknowledgments) were consulted to determine extents of occurrence and variation of characters, including the presence of wing bands in both sexes. The collections of MRAC, MZUF, RMNH, SMNS, and ZMUH were completely revised, as was the Consiglio material from Ethiopia in MZUL (see Pinhey 1982). Altogether data of 1,154 males and 970 females were obtained. A few records were verified from photographs.

Two syntopic males from Senegal (see Table 2) were investigated more closely with light and scanning electronic microscopy. Animals were fixed and stored in 70% ethanol. External morphology was examined under a stereo-microscope to find distinguishing characters. Afterwards three basal and three terminal segments of the abdomen were macerated in 10% KOH, vesicae spermalis were extracted, and all cuticular parts were examined in glycerine under a stereo-microscope. For SEM study these parts of the abdomen were washed in distilled water, dehydrated in a graded ethanol series and in acetone, critical point dried (OM CPD 7501), sputtered with gold-palladium (OM-SC7640), and examined with a Zeiss EVO-50 SEM. Reproductive structures were compared following Miller (1982, 1988).

Abbreviations for collections:

- ISNB — Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
- MLUH — Wissenschaftsbereich Zoologie, Martin-Luther-Universität, Halle, Germany
- MRAC — Musée Royal de l'Afrique Centrale; Tervuren, Belgium
- MZUF — Museo Zoologico "La Specola", Firenze, Italy
- MZPW — Museum of the Institute of Zoology, Polish Academy of Science, Warszawa, Poland
- MZUL — Museo di Zoologia dell'Università "La Sapienza", Rome, Italy
- RMNH — Nationaal Natuurhistorisch Museum Naturalis, Leiden, The Netherlands
- SMNS — Staatliches Museum für Naturkunde, Stuttgart, Germany
- ZMHB — Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
- ZMUH — Zoologisches Institut und Zoologisches Museum der Universität von Hamburg, Germany.

TAXONOMY

Males could be unambiguously assigned to two morphotypes (Table 1). Only one male type was found at most localities, with the first mainly in the northern half of Africa and adjacent Eurasia, and the second mainly in the south and Madagascar (Figs 2, 3). As no intermediates were found among 1,154 males examined across a huge geographic and environmental range, and also because the two occurred together at the same place and time of year (Table 2) we considered that the observed morphotypes represented two separate species.

Table 1. Differences between the two species treated here. * similar but less prominent on S7; ** records from Angola, Central African Republic, Congo-Brazzaville, Equatorial Guinea (Bioko), Togo, and Yemen were not verified

Character	<i>Brachythemis impartita</i>	<i>Brachythemis leucosticta</i>
Male venation, dorsal view (Fig. 7)	Anterior and posterior borders of Pt proximally pale, as are veins posterior to Pt; veins in costal and discoidal fields often pale, concolorous with subcostal veins	Borders of Pt dark, as are veins posterior to it and in costal and discoidal fields, thus contrasting with pale subcostal veins
Cells in Hw discoidal field (Fig. 6)	Average 89.5 (range 67-121), 80% with 75-110	Average 76.4 (range 63-86), 87% with 70-85
Wing bands in males: in females:	Always present Frequent in many populations, but virtually absent in N of range	Absent when teneral Very infrequent and probably most often absent
Hamular hook (Fig. 9a) and antero-external border of its basal pad in ventral view (Fig. 9b)	Hook longer, antero-external border of pad squarely rounded	Hook shorter, antero-external border of pad evenly rounded
Genital lobe	Often largely pale, even in darker males	Always largely dark, even in paler males
Male ventral portion of tergite S8 (Fig. 8a)	2.4-2.8 times as long as wide	1.8-2.3 times as long as wide
Male ventral carinae S8* (Fig. 8a)	Straight, at most slightly kinked, with few dispersed denticles	Medially with a kink or lobe marked by dense denticles
Male epiproct (Fig. 8c)	Usually reaching well distally to ventral tooth of cerci	Reaching to or just distally to ventral tooth of cerci
Confirmed range, also from photographs** (Figs 2, 3)	Algeria, Benin, Burkina Faso, Cameroon, Chad, Congo-Kinshasa, Côte d'Ivoire, Cyprus, Egypt, Ethiopia, The Gambia, Ghana, Guinea-Bissau, Guinea-Conakry, Israel, Italy (Sardinia, Sicily), Jordan, Kenya, Mali, Mauritania, Morocco, Niger, Nigeria, Portugal, Saudi Arabia, Senegal, Spain, Sudan, Syria, Tanzania, Tunisia, Turkey, Uganda, Western Sahara	Benin, Botswana, Burkina Faso, Burundi, Congo-Kinshasa, Ethiopia, The Gambia, Ghana, Kenya, Madagascar, Malawi, Mozambique, Namibia, Niger, Senegal, Somalia, South Africa, Rwanda, Tanzania, Uganda, Zambia, Zimbabwe

Nomenclature

Probably due to the familiarity of *B. leucosticta*, only three valid species-group names and one nomen nudum have been introduced to refer to these two species, all before 1900:

Libellula leucosticta Burmeister, 1839: 849 (lectotype: Port Natal [= Durban], South Africa; MLUH).

Libellula unifasciata Rambur, 1842: 108 (type male: Egypt; type female: Senegal; ISNB).

Libellula fasciata Rambur, in litt. (ISNB); nomen nudum.

Zonothrasys impartitus Karsch, 1890: 297 (holotype: Benue, Cameroon; lost – neotype designated here: Ngaoundaba Ranch, Cameroon; RMNH).

Burmeister (1839) described *L. leucosticta* "vom Port natal ... auch in Aegypten und Senegambien" but Calvert (1898) selected a South African male as the "actual type". The specimen is in good condition and has labels: "Considered by me as Burmeister's type of his *Libellula leucosticta* P.P. Calvert. May 1896" [white] and "*Leucosticta* Burmeister. Port. nat. Drg." [blue]. It conforms with the southern species (V. Clausnitzer pers. comm.).

The Egyptian male type of *L. unifasciata* (not examined) probably conforms with the northern species and could be selected as its lectotype. That name is, however, unavailable because it is a homonym of *L. unifasciata* DeGeer, 1773 – a junior synonym of *Erythrodiplax umbrata* (Linnaeus, 1758) (see Ris 1911a: 484, 1911b: 585).

The female holotype of *Z. impartitus* originated from N Cameroon (Fig. 4). This is within the potential range of both species, but females of the two could not be reliably separated. The type could, moreover, not be found either in ZMHB or MZPW, where material described by Karsch and collected by Dohrn is expected (D. Mierzwa, M. Ohl pers. comm.). However, the holotype had wing bands ("zwischen dem Innenrande des Pterostigma und dem Nodus sind auf allen Flügeln die Queradern ... braun gesäumt"), and based on the frequency of banded females, the chance that it belonged to the northern species is estimated at 60%, against less than 3% for the southern one. Thus we consider *Brachythemis impartita* (comb. nov.; corrected spelling) as the northern species, also because the latter predominates in this part of Africa (Fig. 2). To avoid any confusion of these similar species, and in accordance with Art. 75.1-4 of the Code (International Commission on Zoological Nomenclature 1999), a male from near the type locality must be selected as neotype. Attempts to obtain new specimens from the Benue in Cameroon failed (R. Buij, B. Croes, J. van der Waarde pers. comm.) and therefore a male collected by J. van der Waarde ca 240 km south at Ngaoundaba Ranch near Ngaoundéré, Cameroon on 24 xii 2008 (RMNH) was selected as neotype (present designation), which conforms with the diagnosis of *B. impartita* in Table 1.

The name *impartita* (undivided), although referring originally to the condition of the Fw triangles and subtriangles, is suitable because it hints at the species' history of obscurity. As both species are internationally known by the vernacular name 'Banded Groundling' (e.g. Dijkstra & Lewington 2006; Samways 2008), we propose the prefixes 'Northern' and 'Southern' to distinguish them.

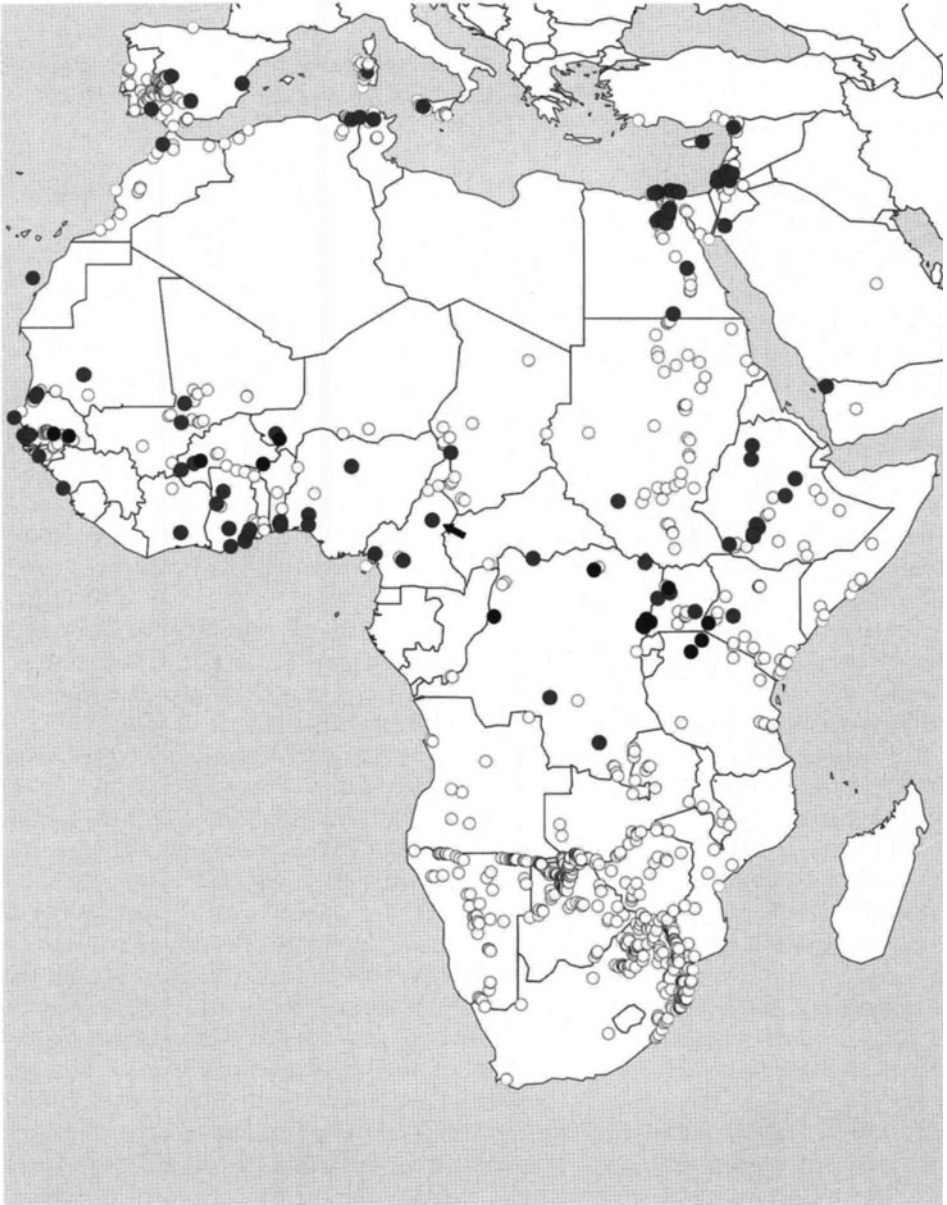


Figure 2: Confirmed distribution of *Brachythemis impartita*, based on examined males (grey circles; black where occurs with *B. leucosticta*), and records without species information from the databases maintained by J.-P. Boudot and J. Kipping (open circles) — the arrow indicates locality of neotype. Two southernmost records in Congo-Kinshasa must be confirmed (see text p. 251).

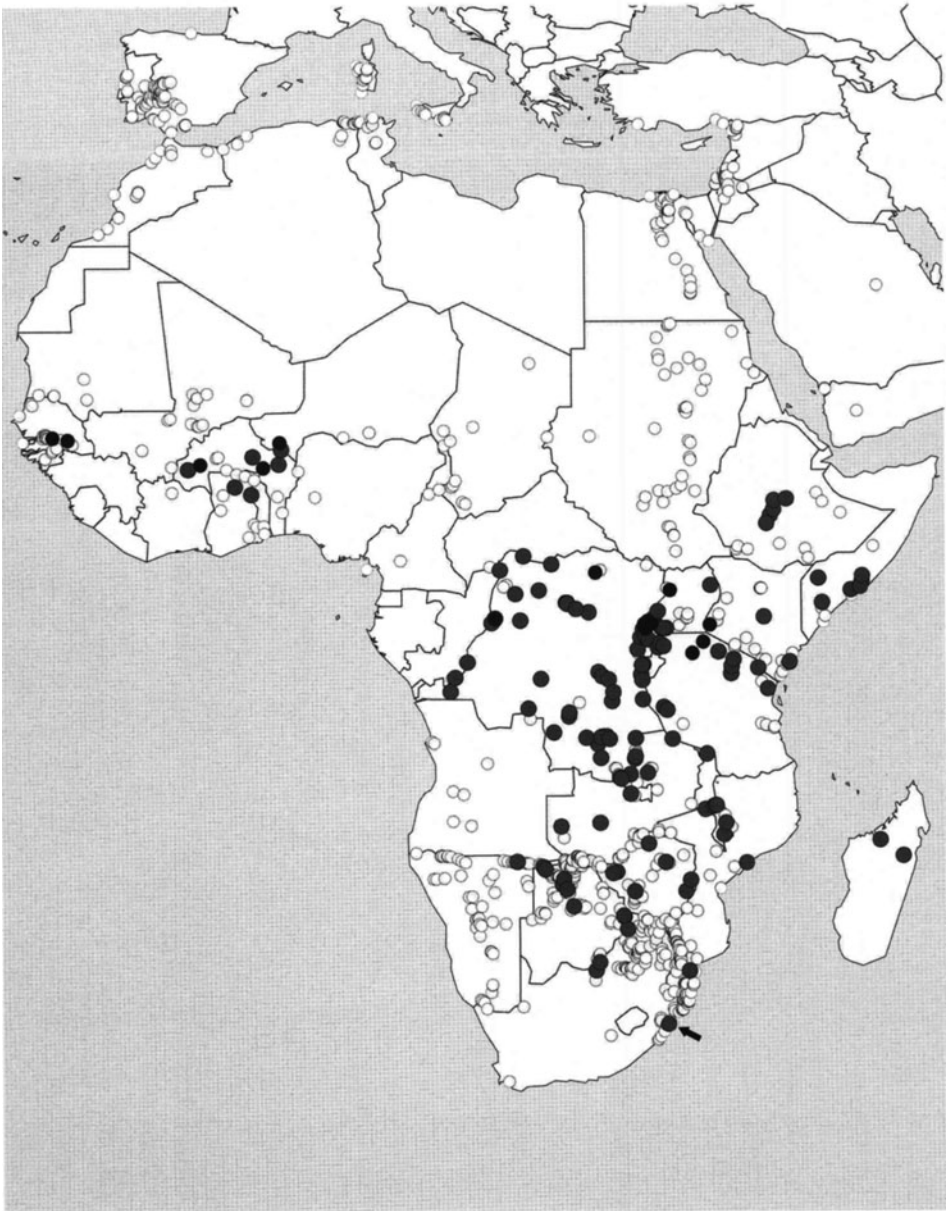


Figure 3: Confirmed distribution of *Brachythemis leucosticta*, based on examined males (grey circles; black where occurs with *B. impartita*), and records without species information from the databases maintained by J.-P. Boudot and J. Kipping (open circles) — the arrow indicates locality of lectotype.

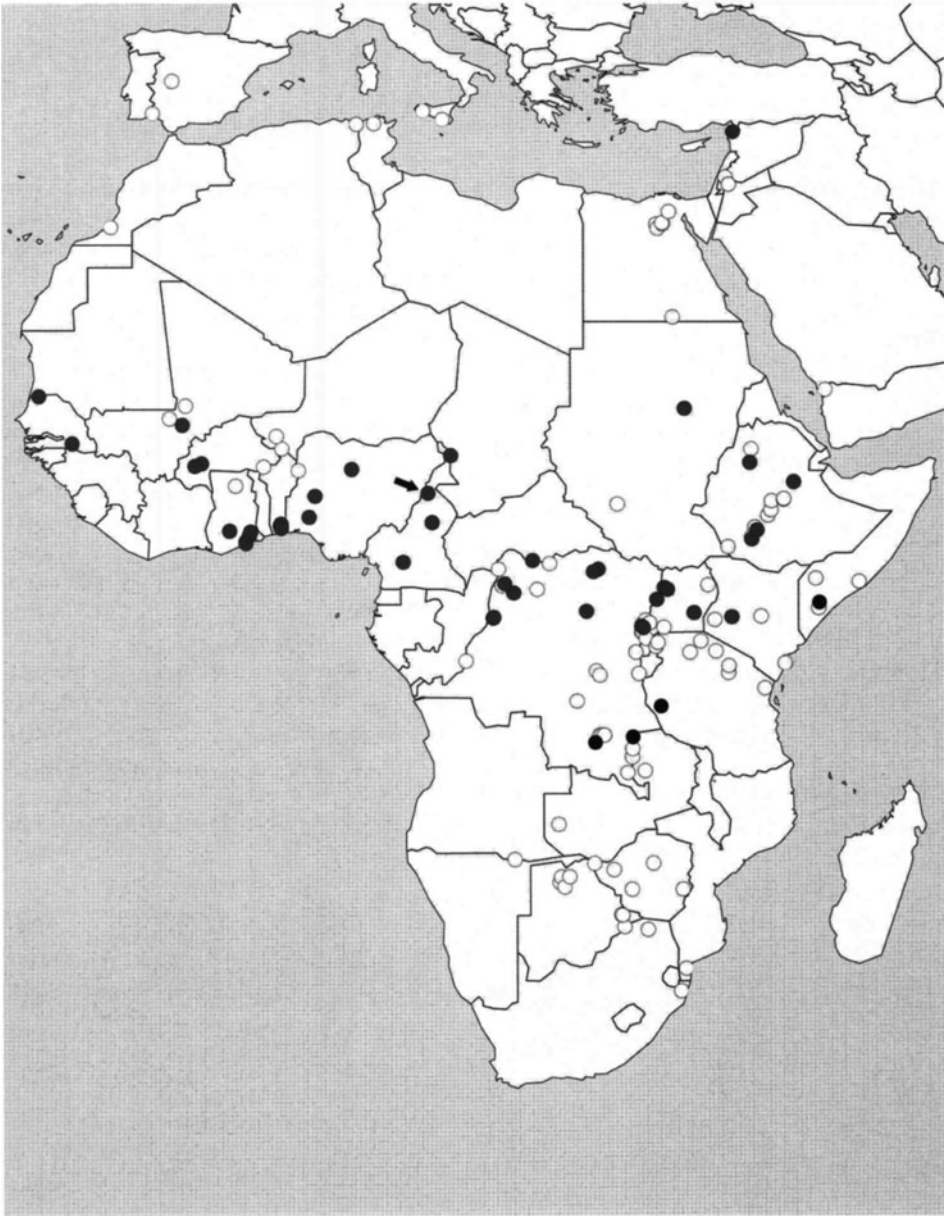


Figure 4: Distribution of wing bands in females of the two *Brachythemis* species, based on examined females — open circles: all females not banded; grey circles: one or more females banded, within confirmed range of *B. impartita* (arrow indicates locality of its holotype); black circles: banded females outside confirmed range of *B. impartita*.

Description of male neotype of *Brachythemis impartita*

Head: Labium and face pale brown, becoming darker dorsally to glossy blackish bases of frons and vertex. Antennae and small lateral marking on frons black. Occipital triangle dark brown. Back of head brown, postgenae narrowly black along dorsal half of eye margin and with some dark markings. Eyes dark brown.

Thorax: Prothorax brown covered with grey pruinosity, posterior lobe small. Synthorax, including venter, brown covered with thick grey pruinosity that obscures an intricate pattern of black lines. Legs black, densely pruinose on coxa and thinly on femora, with pale brown lines over full length of exterior surfaces of tibiae, as well as some pale brown on inner surfaces of fore and hind femora.

Wings: Clear, each wing with dark brown band between node and Pt. Venation mostly dark brown, but cross-veins in costal, subcostal, radial, cubital, and discoidal fields of antenodal part of wings pale yellowish, as are bases of costa and sectors of arculus, and arculus itself. In the postnodal part of the wings, a field of veins in the clear area posterior to Pt also pale. Pt dorsally cream with brown distal end; borders dark brown, with proximal three-quarters of anterior border and two-thirds of posterior border pale. Arculus placed at one third of distance from Ax1 and Ax2. In Fw $7\frac{1}{2}$ Ax and 7 Px, in Hw 6 Ax and 6-7 Px. Bridge and cubital spaces each with a single cross-vein in all wings. All triangles, subtriangles, and supradiangles uncrossed. Fw discoidal field parallel-sided and largely of three cell-rows. Rspl subtending 4 doubled cells in both Fw, 2 in both Hw. Anal loop of 17-19 cells.

Abdomen: Blackish, browner on sides, with pruinosity laterally on S1-3 and ventrally to S8. Secondary genitalia and genital lobe largely brown, set off from darker surroundings. Ventral carinae of all segments straight with dispersed denticles. Appendages pale brown, darker towards tips, cerci with black ventral teeth; epiproct clearly surpasses ventral angle of cerci.

Measurements [mm]: Total length 31.8, abdomen length 19.4, Fw length 25.0, Hw length 24.5, Pt in Fw 3.0.

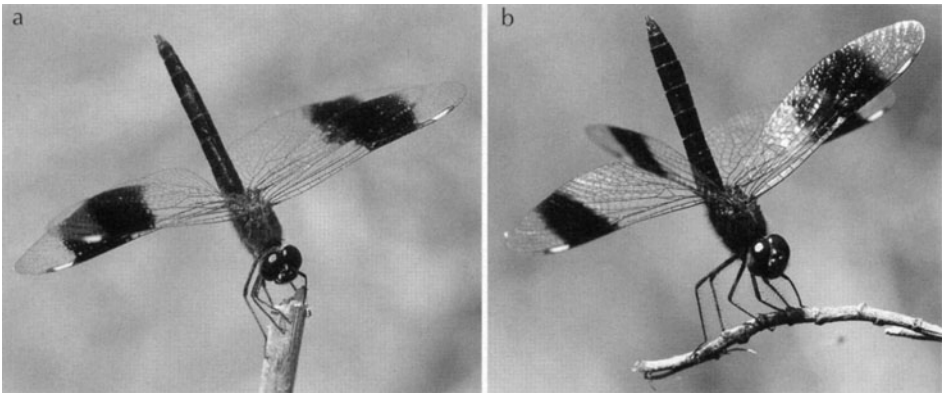


Figure 5: Habitus of *Brachythemis impartita* and *B. leucosticta*. Note the subtle differences: the grayer look of *B. impartita*, the paler venation especially under Pt, the more slender abdomen end and the slightly more parallel cerci — (a) mature male *B. impartita* from Sardinia, Italy; (b) mature male *B. leucosticta* from Uganda. Photos by Jean-Pierre Boudot (a), Hans-Joachim Clausnitzer (b).

Diagnosis

Of the characters presented in Table 1, the structure of S8 and coloration were most useful for identification of the two species. The paleness of the venation and genital lobe was variable, but at least the veins below the Pt invariably stood out palely in *B. impartita* (Fig. 7a), as did often (but not always) the tip of the lobe. Also the ventral carinae of S8 varied somewhat: a straight and rather bare carina was confined to *B. impartita* (Fig. 8a left); one with a prominent denticulate lobe to *B. leucosticta* (Fig. 8a right). A slight kink in the carina of *B. impartita* could approach a weakly developed lobe in *B. leucosticta*, but the former would never bear a concentration of denticles. The venation was denser (i.e. more cells per space) in *B. impartita*, as expressed by the number of cells in the Hw discoidal field (i.e. between the triangle, MA, CuP, and wing border). However, overlap was extensive and *B. impartita* was especially variable (Fig. 6).

Structural differences in secondary genitalia were very slight. We found none in the vesica spermalis (Fig. 9c) and the small difference in the hamule could only be appreciated by direct comparison (Figs 9a, b). The relative length of the epiproct was often hard to judge due to variation and distortion (Fig. 8c). The cerci of *B. leucosticta* could be more curved and wider apart at their bases in dorsal view, but could also be straight and rather parallel as in *B. impartita*. Certainly the differences between the Wassadou males were extreme (Fig. 8b).

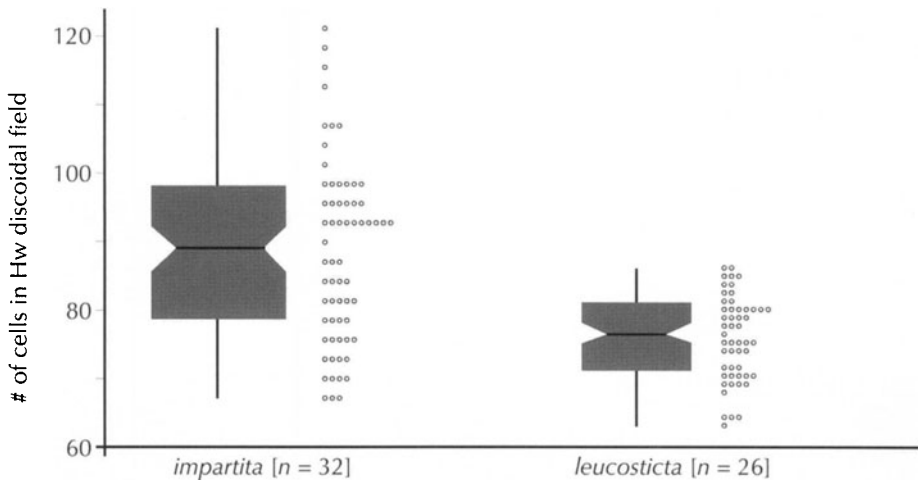
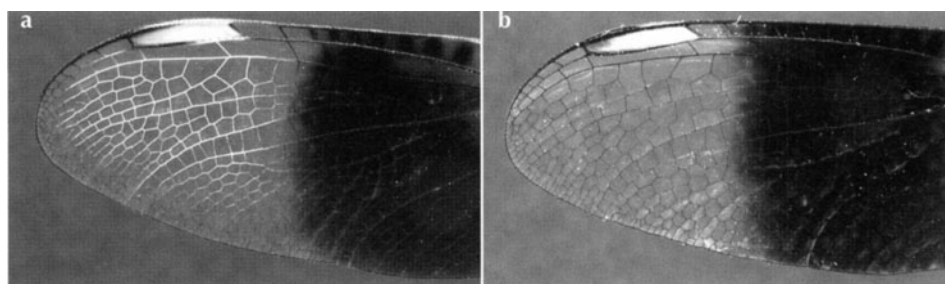


Figure 6: Box-Whisker-Dots plot of the number of cells in the Hw discoidal field of the two *Brachythemis* species. Both wings of each male in the sample were counted, the specimens originating from throughout the species' ranges, including three sites of syntopy. The dots provide a frequency distribution of the cell counts, the box represents the quartiles of data above and below the median, the whiskers their total range, and the dash their mean. The height of the notch is the t -test confidence interval about the median ($p = 0.05$). The species' notches do not overlap, which indicates their cell counts are significantly different.

Table 2. Syntopic material of the two species treated here, sorted from west to east. *nBi*: numbers of males of *Brachythemis impartita*; *nBl*: numbers of males of *B. leucosticta*.

Country/Locality	Date	Leg.; Collection	<i>nBi</i>	<i>nBl</i>
The Gambia				
Gambia River at Sami Bridge	02 xi 1996 (Bi), 03 xi 2000 (Bl)	M.J. Parr; coll. M.J. Parr	1	1
Senegal				
Wassadou, P.N. du Niakolo Koba	17 v 2008	A. Gumovsky; coll. Matushkina	1	1
Burkina Faso				
Lake at Houndé	23 x 1994	J.C. Streito, coll. G. Jacquemin	1	1
Benin				
Arli River in P.N. de la Pendjari	19-20 v 2001	S.L. Tchibozo; RMNH	1	2
Niger				
Niger River at Say	09 ii 1977	H.J. Dumont; MRAC	3	1
Congo-Kinshasa				
Eala	xii 1934-ii 1935	J. Ghesquière; MRAC	2	13
Bambesa	vii-ix 1933	H.J. Brédo; MRAC	2	1
Lake Edward at Kamande	04-11 v 1935, 18 xi 1935	H. Damas; MRAC	35	10
Lake Edward at Kimboho	26-28 xi 1935	H. Damas; MRAC	28	4
Lake Edward at Vitshumbi	27 ix-24 x 1935	G.F. de Witte; MRAC	7	99
Lake Edward at Isango	01-04 vi 1935, 05-14 xii 1935	H. Damas; MRAC	2	1
Lake Albert at Mahagi-Port	x 1934	H.J. Brédo; MRAC	26	1
Uganda				
Lake Edward at Kisenyi	17 vi 1935	H. Damas; MRAC	1	5
Tanzania				
Lake Victoria at Mwanza	1983-1986	P.C. Goudswaard; RMNH	23	38
Lake Victoria at Mgongo	20-24 iii 1952	E. Lindner; SMNS	1	2
Kenya				
Lake Victoria at Mbita	26-28 x 1997	N. Minakawa; coll. D.R. Paulson	3	2

Figure 7: Fw tip of *Brachythemis* males — (a) *B. impartita* Karnak, Egypt; (b) *B. leucosticta* Krogue, Tanzania.

Although the two species were not recognised for 170 years, also Burmeister must have had both, they were separable from photographs and must also be on the wing (Fig. 5). The paler venation below the Pt was usually visible in photographs of *B. impartita*, or rather invisible as the veins faded with the background. Moreover, its mature males appeared greyer because of a browner (rather than black) undertone overlaid by somewhat more pronounced pruinosity.

None of the male characters applied well to females and no reliable distinction for that sex was found. The Pt borders tended to be paler in assumed *B. impartita* females, as did some other veins, but this was much less pronounced. The different ventral structures of S7-8 in males suggest that the anterior and dorsal part of the female head may differ in the two species. The vertex of suspected *B. leucosticta* females seemed less swollen, but this was inconsistent.

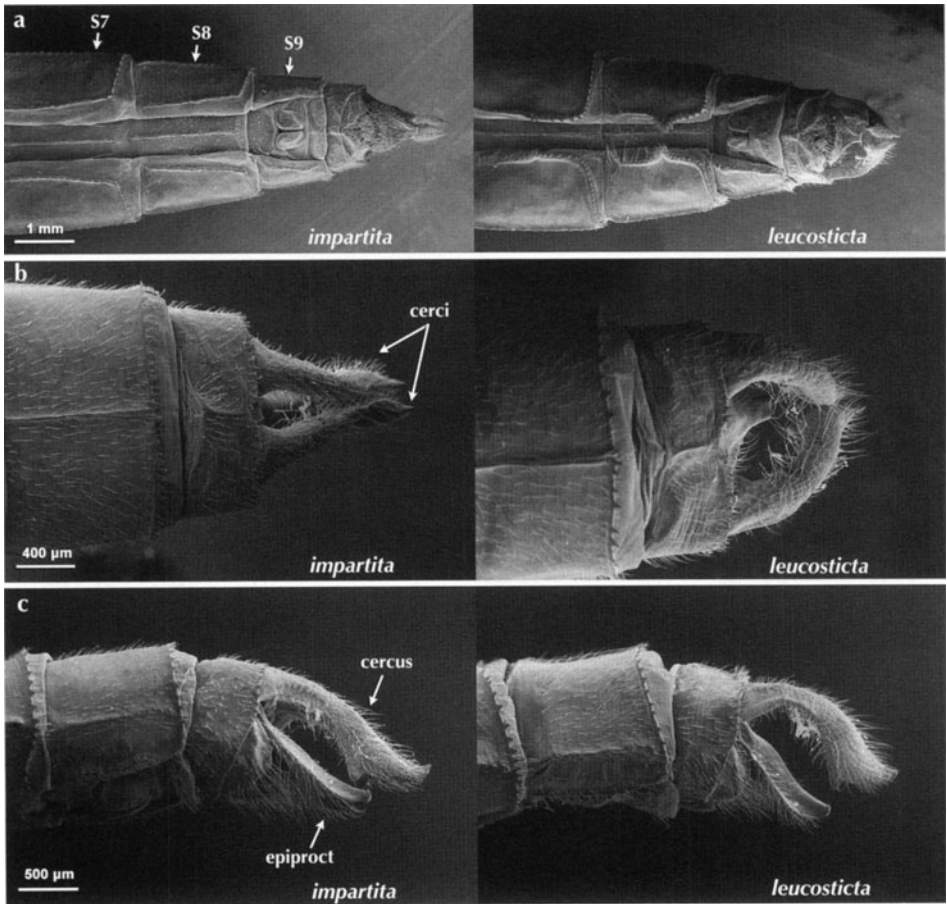


Figure 8: Scanning electron micrographs of terminal segments of abdomen of *Brachythemis impartita* (left) and *B. leucosticta* (right) males from Wassadou, Senegal — (a) S7-9 in ventral view; (b-c) S9-10 in dorsal and lateral view respectively.

Wing banding

According to Pinhey (1982), in Ethiopia "all males (51 examined by us, from which 73% were *B. impartita*) were found to be banded, even juveniles and teneral. In southern Africa tenerals (all likely *B. leucosticta*) tend to be without bands, juveniles developing fasciae in stages." Near Zaria, Nigeria "males always seem to have a

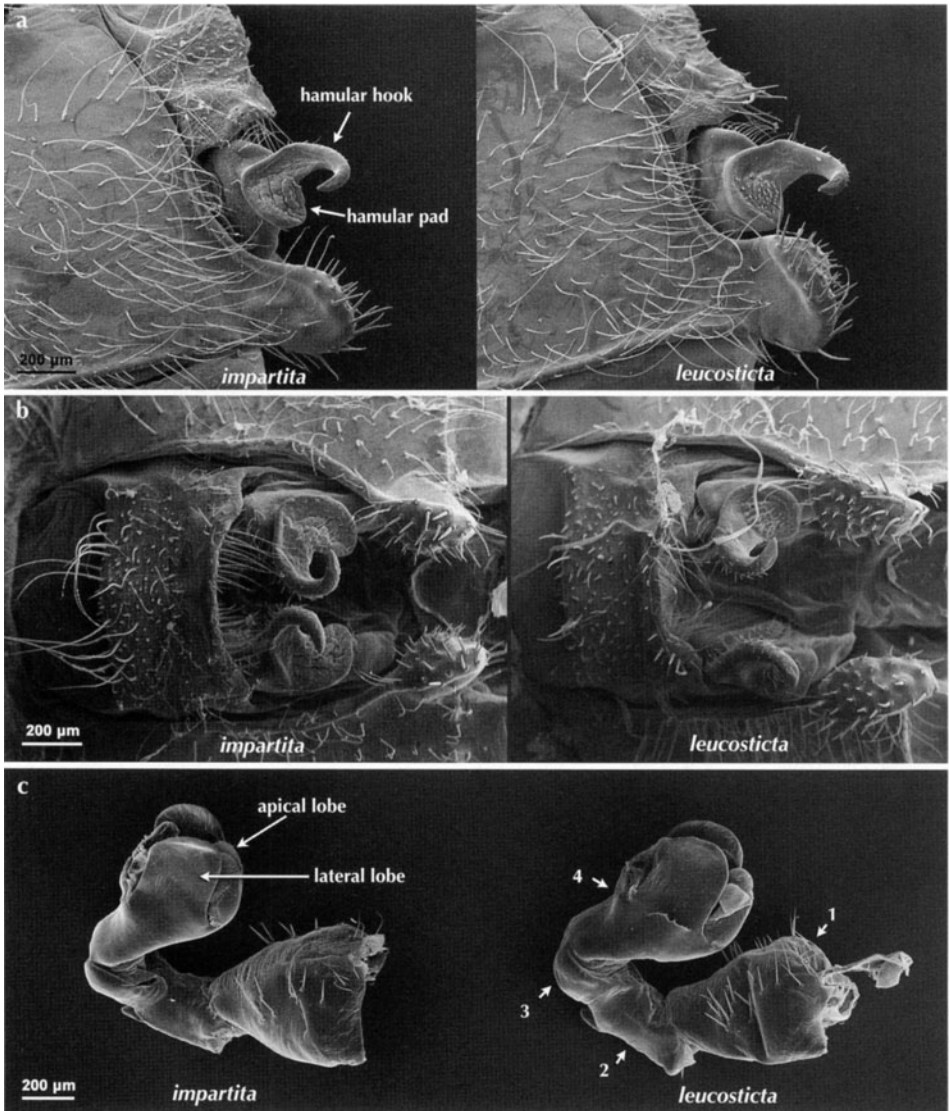


Figure 9: Scanning electron micrographs of secondary genitalia of *Brachythemis impartita* (left) and *B. leucosticta* (right) males from Wassadou, Senegal — (a) genital fossa in lateral view; (b) genital fossa in ventral view; (c) vesica spermalis in lateral view (extracted from body, segments numbered).

band" (Adetunji & Parr 1974) and at Khartoum, Sudan "immature males have pale wing spots" (Happold 1968). These populations must belong to *B. impartita*. Indeed all examined *B. impartita* males ($n = 374$), including four from Zaria (M.J. Parr pers. comm.), had at least an indication of a band, with the exception of one collected at emergence in Morocco (J.-P. Boudot pers. comm.). However, 9.1% of *B. leucosticta* males ($n = 770$), all teneral, had no hint of a band (but see Fig. 10).

Around the Mediterranean Sea, where only *B. impartita* occurs, females appear not to develop wing bands (Jödicke et al. 2000). Examined females from Egypt, Italy, Israel, Jordan, Morocco, Spain, and Tunisia ($n = 39$) were indeed not banded. Nonetheless, a single female from Algeria (RMNH, no further details) and one photographed in S Turkey (G.J. van Pelt pers. comm.) had faint bands. Not one Mwanza female ($n = 37$) was banded, suggesting *B. impartita* females are clear-winged there, like *B. leucosticta*. However, most of the 119 females with at least indications of bands (12.2% of 970 examined) originated from within the geographic range of *B. impartita*: of females found with *B. impartita* males 22.1% ($n = 420$) were banded versus only 4.5% ($n = 726$) of females found with *B. leucosticta* males. These values were 38.7% ($n = 191$) and 2.8% ($n = 497$) with sites of proven syntopy excluded (Table 2). At Ethiopian lakes with only *B. impartita* males, 34.6% of females were banded ($n = 52$), while all 17 females from lakes with only *B. leucosticta* males were unbanded. Banded females were notably frequent in regions dominated by *B. impartita*: 60.2% in sub-Saharan W Africa ($n = 83$, Senegal to Chad), 61.8% on the W shore of Lake Albert ($n = 34$), and even 69.7% in Ghana ($n = 33$). In probably pure *B. impartita* populations at Khartoum "a few mature females possessed wing markings" (Happold 1968), while near Zaria 37% of 145 females had wing bands, irrespective of maturity (Adetunji & Parr 1974).



Figure 10: Mature male *Brachythemis leucosticta* photographed near Gaborone, Botswana, on 08 December 2008. The clear wings typical of teneral males of this species were somehow retained in the right pair of this individual. Photo by Karen Conniff.

Therefore, wing banding was informative, apparently being absent in males of *B. leucosticta* for some time after emergence, but not in those of *B. impartita*. Banded females seemed virtually absent in *B. leucosticta* and in peripheral populations of *B. impartita*, but frequent throughout the core-range of *B. impartita*. The most southern and eastern records of banded females, although associated with *B. leucosticta* males, were not too far beyond the range of *B. impartita* and could potentially belong to the latter species (Figs 2-4). However, not many females were studied from many peripheral regions where one of the two species occurs and banded females may thus have gone undetected there.

Distribution

Various geographic and possibly ecological patterns emerged from the data: *B. leucosticta* was recorded in most of sub-Saharan Africa and Madagascar, and *B. impartita* in a wide ring around the Sahara extending N of the Mediterranean Sea and E across the Red Sea (Figs 2, 3). Two single *B. impartita* males from Kananga and Kalumegongo in S Congo-Kinshasa, found among 188 *B. leucosticta* males in MRAC, must be considered with some caution, as mislabelling may have occurred. Nonetheless, the two species overlapped widely from the Gambia River to Lake Victoria (Figs 2, 3; Table 2). In sub-Saharan W Africa, 84% of males ($n = 99$, Senegal to Chad) pertained to *B. impartita*, and *B. leucosticta* seemed to occur most on large savannah rivers like the Arli, Gambia, Mékrou, Niger, Oti, and White Volta. Ethiopian records originated mainly from the many large lakes and not a single case of co-occurrence was found among 74 examined males (77% *B. impartita*). Although sample sizes were negligible, the data suggested the two occupy different lakes: *B. leucosticta* was found at Awash ($n = 4$), Hora (2), Ziway (6), Langan (4), and Awasa (1), and *B. impartita* only at Tana (6), Basaka (1), Abaya (25), and Chamo (10). In C Africa, *B. leucosticta* predominated throughout, with the exception of the large lakes: in Congo-Kinshasa, 70% of males ($n = 247$) obtained around Lake Edward and only one male ($n = 54$) at Lake Albert were of that species, against 96.5% elsewhere in the country ($n = 315$). Also on the S and E shores of Lake Victoria *B. impartita* was relatively abundant (39% of 71 males).

Seasonality

Only long series of restricted geographic origin provided some indication of flight periods. The 61 males studied from Mwanza on Lake Victoria, comprised 62% *B. leucosticta*, and were collected in all months except January, July, October, and December. In February only a single *B. impartita* was taken, but otherwise both species were obtained in all months. The sample is insufficient for definitive conclusions, but proportionately more *B. leucosticta* were collected in June-September (22 specimens vs only three of *B. impartita*) and *B. impartita* in November-May (20 vs 16 of *B. leucosticta*), corresponding with the driest period in June-September and the wettest in November-April respectively. Similarly, 73% of 79 males collected in Virunga NP, Congo-Kinshasa (mostly on Lake Edward) in April-July were *B. leucosticta* and 78% of 59 males in November-December were *B. impartita*. However, collecting in the park was patchy in time and space: a series of 107 specimens from September-October (93% *B. leucosticta*) were all but one from a single site.

DISCUSSION

Taxonomic status

Do the observed morphotypes represent separate species, or merely forms or phenotypes of a single species? It is unlikely that their differences are phenotypic as no intermediates were found in a large, geographically and environmentally diverse sample, also when and where both were present. Although adults might be active in different seasons locally, only one type occurs in most regions with marked dry and wet seasons. Moreover, both are found from deserts to rainforests within a defined geographic range: so that it is location, and not environment, which largely determines what type is present where. We believe that subspecies cannot occur together by definition and therefore the clear, but not complete or nested, distributional overlap supports a status of the two as species. Their status must, however, be investigated further, firstly with molecular techniques. The genus *Brachythemis* forms a distinctive monophyletic group with *Tholymis* and *Zyxomma*, but determining the exact positions of the possibly and probably synonymous monotypic genera *Parazyxomma* and *Deielia* requires genetic sampling of all *Brachythemis* species (Dijkstra 2003; Ware et al. 2007; Pilgrim & von Dohlen 2008). Given the broad geographic overlap, it is also interesting to study the ecological niche partitioning, reproductive isolation mechanisms, and historical biogeography of the two species. These subjects are touched on below, but behavioural observations are lacking, particularly with regards to the possible reproductive function of the ventral structure of male S7-8.

Remarks on larvae

Corbet (1957) noted “wide variability ... depending, it seems, on the type of bottom over which the larvae live”. At exposed sandy shores “the abdomen is more or less cylindrical, and the lateral spines are small and point posteriorly” and “the colour is almost invariably pale”. In larvae found over muddy bottoms “the abdomen becomes more triangular in cross-section, short, broad and dark, while the lateral spines are large and project more laterally”. Although “intermediate forms exist in habitats where mud and sand lie close together”, this may indicate that the two species, probably both present in Corbet’s material, differ in larval ecology and morphology. In Namibia only the ‘mud form’ and *B. leucosticta* occur (F. Suhling pers. comm.), while assumed *B. impartita* exuviae from Sardinia and Tunisia are near the ‘sand form’ (J. Arlt, O. Brauner, B. Kunz, M. Lohr, C. Vanappelghem pers. comm.). Corbet’s hypothesis of environmental forms predicts the presence of intermediates, and thus morphological extremes of both species may have been interpreted as such.

Ecology and biogeography

Despite the possible differences observed, the two species probably have similar ecologies. Corbet & Miller (1991) aptly described it: “Adults occur near lakes, large ponds and reservoirs [also rivers] but are usually uncommon or absent at bodies of water less than about 20-30 m in diameter. They prefer exposed parts of lake shores and tend to avoid places with many bushes or trees. They often perch on bare ground such as rock, mud or sand and less often on vegetation, except for emergent plants over water.” Of 59 photographed individuals examined (both species), 43% perched directly on the ground, 37% low on vegetation (mostly dead), and 20% on other

slightly raised surfaces (mostly rocks). Although habitats are always open, both species range from some of Africa's driest regions to the wettest, e.g. from the borders of the Sahara (*B. impartita*) and Kalahari (*B. leucosticta*) to the Congo Basin (both). Possibly in the area of overlap *B. impartita* is more partial to large lakes, sandy bottoms, and adult activity in the wet season, and *B. leucosticta* to rivers, mud, and the dry season, but current evidence to confirm this is scanty and circumstantial. Because most material was obtained in a single month the species' possible segregation on Ethiopian lakes cannot be explained by seasonality, but perhaps by ecological factors or colonisation history.

The origin of the two species, their ranges, and current coexistence may be related to Africa's climatic variability, especially in the last eight million years (see Dijkstra 2007a for an overview). The simplest scenario is by allopatric divergence in open habitat north and south of a transcontinental rainforest belt in a wetter period, with ranges shifting to meet each other in drier times. Only 8,000-9,000 years ago the Sahel and Sahara were dotted with lakes and swamps, allowing for expansion across N Africa, with subsequent aridification leading to the presently peripheral distribution. The wide distributions, also on islands and at isolated desert sites, can also be attributed to a strong dispersal capacity. This is illustrated by a male of *B. impartita* caught at light on a steamer "200 miles" (presumably nautical) off Gran Canaria on 28 October 1970 (RMNH). The precise position is unknown, but the distance (= 370 km) is substantially greater than the 200 km between the island, where the species does not occur, and the mainland. Calvert (1893) reported a male from the desert island São Vicente, Cape Verde. This island lies 830 km off the mainland, the archipelago 570 km, but the record is unconfirmed (Aistleitner et al. 2008). The expansion of *B. impartita* is illustrated by its first discovery in Europe in Portugal in 1957, Spain in 1961, and Sardinia in 1979 (Crucitti et al. 1981); it was found in Cyprus in 2006 (Cottle 2007).

EPILOGUE: CRYPTIC LIBELLULIDS

Once again, one of Africa's most familiar and longest known dragonfly 'species' was found to conceal multiple species after prolonged taxonomic inertia. The most striking case is that of the 'former forms' *Palpopleura lucia* (Drury, 1773) and *P. portia* (Drury, 1773), the first odonates to be named from African soil (Dijkstra et al. 2003). Besides differences in size and wing markings reviewed by O'Neill & Paulson (2001) they differ genetically (Mitchell & Samways 2005) and in vesica spermalis morphology and pruinosity pattern (KDBD unpubl.; Karsch 1894). Their status as forms of one species may have been maintained for almost a century by their seemingly complete geographic and ecological overlap. The confusion surrounding *Diplacodes lefebvrii* (Rambur, 1842), *D. deminuta* Lieftinck, 1969, and *D. pumila* Dijkstra, 2006 was only resolved in steps (Pinhey 1967; Lieftinck 1969; Pinhey 1976; Dijkstra 2006). The characters and distribution of *Nesciothemis pujoli* Pinhey, 1971 – the western counterpart of the widespread *N. farinosa* (Förster, 1898) – are not yet resolved (O'Neill & Paulson 2001; Dijkstra 2007b). Despite morphological and ecological differences and extensive range overlap, *Rhyothemis fenestrina* (Rambur, 1842) and *R. notata* (Fabricius, 1781) were treated as synonyms or subspecies (KDBD unpubl.). Finally, structural differences 'within' *Trithemis stictica* (Burmeister, 1839) were only discovered once that 'species' was found to be genetically het-

erogeneous (Damm & Hadrys 2009). All cases demonstrate how deceptive appearances are and why closer inspection of ‘common’ and ‘recognisable’ species is warranted. What might *Acisoma panorpoides* Rambur, 1842, *Chalcostephia flavifrons* Kirby, 1889, *Hemistigma albipunctum* (Rambur, 1842), *Olpogastra lugubris* Karsch, 1895, *Urothemis edwardsii* (Selys, 1849), and *Zygonyx torridus* (Kirby, 1889) – to name a few – still conceal?

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REFERENCES

- Adetunji, J.F. & M.J. Parr, 1974. Colour change and maturation in *Brachythemis leucosticta* (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 3: 13-20.
- Aistleitner, E., W. Barkemeyer, G. Lehmann & A. Martens, 2008. A checklist of the Odonata of the Cape Verde Islands. *Mitteilungen des Internationalen Entomologischen Vereins*, Frankfurt a.M. 33: 45-57.
- Burmeister, H., 1839. *Handbuch der Entomologie. Zweiter Band. Besondere Entomologie. Zweite Abtheilung. Kaukerfe. Gymnognatha. (Zweite Hälfte; vulgo Neuroptera).* T.C.F. Enslin, Berlin.
- Calvert, P.P., 1893. Order Pseudoneuroptera. In: Riley, C.V. (ed.) “Scientific results of the U.S. Eclipse Expedition to West Africa, 1889-’90. Report upon the Insecta, Arachnida, and Myriapoda”. *Proceedings of the United States National Museum* 16 (951): 582-586.
- Calvert, P.P., 1898. Burmeister’s types of Odonata. *Transactions of the American Entomological Society* 25: 27-104.

- Corbet, P.S., 1957. Larvae of East African Odonata. 6-8. 6. *Brachythemis lacustris* Kirby, 7. *Brachythemis leucosticta* (Burmeister), 8. *Zyxomma flavicans* (Martin). The Entomologist 90: 28-34.
- Corbet, P.S., 1959. Notes on the insect food of the Nile Crocodile in Uganda. Proceedings of the Royal Entomological Society of London (A) 34: 17-22.
- Corbet, P.S., 1999. Dragonflies: behaviour and ecology of Odonata. Harley Books, Colchester.
- Corbet, P.S. & P.L. Miller, 1991. 'Accompanying' behaviour as a means of prey acquisition by *Brachythemis leucosticta* (Burmeister) and other Anisoptera. Odonatologica 20: 29-36.
- Cottle, N., 2007. *Brachythemis leucosticta* (Burmeister, 1839) (Anisoptera: Libellulidae): a new dragonfly species for Cyprus, and *Trithemis arteriosa* (Burmeister, 1839) (Anisoptera: Libellulidae): a rarely recorded dragonfly species in Cyprus. Bulletin of the Amateur Entomologists' Society 68: 59-63.
- Crucitti, P., P.A. Galletti & M. Pavesi, 1981. Un interessante reperto Sardo: *Brachythemis leucosticta* (Burmeister), genere nuovo per la fauna Italiana (Anisoptera: Libellulidae). Notulae Odonatologicae 1: 115-117.
- Damm, S. & H. Hadrys, 2009. *Trithemis morrisoni* sp. nov. and *T. palustris* sp. nov. from the Okavango and Upper Zambezi Floodplains previously hidden under *T. stictica* (Odonata: Libellulidae). International Journal of Odonatology 12: 131-145, pls. III, IV.
- Dijkstra, K.-D.B., 2003. Fooled by the double: *Brachythemis liberiensis* is *Parazyxomma flavicans*, with a note on the Zyxommadini (Odonata: Libellulidae). International Journal of Odonatology 6: 17-21.
- Dijkstra, K.-D.B., 2006. African *Diplacodes*: the status of the small species and the genus *Philonomon* (Odonata: Libellulidae). International Journal of Odonatology 9: 119-132, pls I, II.
- Dijkstra, K.-D.B., 2007a. Demise and rise: the biogeography and taxonomy of the Odonata of tropical Africa. In: Dijkstra, K.-D.B. (ed.) "Demise and rise: the biogeography and taxonomy of the Odonata of tropical Africa", Ph.D. Thesis, Leiden University.
- Dijkstra, K.-D.B., 2007b. The name-bearing types of Odonata held in the Natural History Museum of Zimbabwe, with systematic notes on Afrotropical taxa. Part 1: introduction and Anisoptera. International Journal of Odonatology 10: 1-29.
- Dijkstra, K.-D.B. & R. Lewington, 2006. Field guide to the dragonflies of Britain and Europe. British Wildlife Publishing, Gillingham.
- Dijkstra, K.-D.B., A. Martens & M.J. Parr, 2003. Proceedings of the 1st PHAON Meeting on African Odonata, Gällivare, 26 July 2001. PHAON foreword. African odonatology: past, present and future. Cimbebasia 18: 161-166.
- Happold, D.C.D., 1968. Seasonal distribution of adult dragonflies at Khartoum, Sudan. Revue de Zoologie et de Botanique Africaines 77: 50-61.
- International Commission on Zoological Nomenclature, 1999. International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature, London.
- Jödicke, R., J. Arlt, B. Kunz, W. Lopau & R. Seidenbusch, 2000. The Odonata of Tunisia. International Journal of Odonatology 3: 41-71.
- Karsch, F., 1890. Über Libellulinen der Sammlung des Herrn Dr. Heinrich Dohrn. Entomologische Zeitung, Stettin 51: 295-298.
- Karsch, F., 1894. Libellen von der deutschen Forschungs-Station Yaúnde im Hinterlande von Kamerun, gesammelt von Herrn G. Zenker. Berliner Entomologische Zeitschrift 39: 11-16.
- Lieftinck, M.A., 1969. Odonata Anisoptera. Scientific Results of the Hydrobiological Survey of the Lake Bangweulu - Luapula River Basin 14: 1-61.
- Miller, P.L., 1982. Genital structure, sperm competition and reproductive behaviour in some African libellulid dragonflies. Advances in Odonatology 1: 175-192.
- Miller, P.L., 1988. Similarities in the genitalia and reproductive behaviour of male and female *Tholymis tillarga* (Fabr.), *Parazyxomma flavicans* (Martin), *Brachythemis lacustris* Kirby and *B. leucosticta* (Burm.) (Anisoptera: Libellulidae). Odonatologica 17: 59-64.

- Mitchell, A. & M.J. Samways, 2005. The morphological 'forms' of *Palpopleura lucia* (Drury) are separate species as evidenced by DNA sequencing (Anisoptera: Libellulidae). *Odonatologica* 34: 173-178.
- O'Neill, G. & D.R. Paulson, 2001. An annotated list of Odonata collected in Ghana in 1997, a checklist of Ghana Odonata, and comments on West African odonate biodiversity and biogeography. *Odonatologica* 30: 67-86.
- Parr, M.J., 2009. A few words about Phil Corbet – tribute to Professor Stephen Corbet (21 May 1929 – 13 Feb. 2008) given following the opening ceremony at the 6th WDA International Congress of Odonatology, Xalapa, Mexico, 13 June 2009. *Agrion* 13: 88-89.
- Pilgrim, E.M. & C.D. von Dohlen, 2008. Phylogeny of the Sympetrinae (Odonata: Libellulidae): further evidence of the homoplasious nature of wing venation. *Systematic Entomology* 33: 159-174.
- Pinhey, E., 1967. Odonata of Ngamiland (1967). *Arnoldia Rhodesia* 3 (15): 1-17.
- Pinhey, E., 1976. Dragonflies (Odonata) of Botswana, with ecological notes. *Occasional Papers of the National Museum of Southern Rhodesia (B)* 5: 524-601.
- Pinhey, E., 1982. Odonata collected in Ethiopia. III. Anisoptera. In: "Zoological researches in Ethiopia. Part II. Some results of the first and the second Italian zoological mission to Ethiopia, sponsored by the National Academy of Lincei (1973 and 1975)". *Problemi Attuali di Scienza e di Cultura* 252: 1-56, pl. I.
- Rambur, J.P., 1842. *Histoire naturelle des insectes névroptères. Roret's Suite à Buffon*, Paris.
- Ris, F., 1911a. Libellulinen monographisch bearbeitet. Vol. II. Libellulinen 4. Collections Zoologiques du Baron Edm. de Selys Longchamps. *Catalogue Systématique et Descriptif* 12: 385-528, pl. IV.
- Ris, F., 1911b. Libellulinen monographisch bearbeitet. Vol. II. Libellulinen 5. Collections Zoologiques du Baron Edm. de Selys Longchamps. *Catalogue Systématique et Descriptif* 13: 529-700, pl. V.
- Samways, M.J., 2008. *Dragonflies and damselflies of South Africa*. Pensoft Publishers, Sofia & Moscow.
- Ware, J.L., M.L. May and K.M. Kjer, 2007. Phylogeny of the higher Libelluloidea (Anisoptera: Odonata): an exploration of the most speciose superfamily of dragonflies. *Molecular Phylogenetics and Evolution* 45: 289-310.